TEMPERATURE AND FOOD EFFECTS ON LARVAL PACIFIC HERRING

(*CLUPEA PALLASI)* IN PRINCE WILLIAM SOUND, ALASKA

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TEMPERATURE AND FOOD EFFECTS ON LARVAL PACIFIC HERRING (*CLUPEA PALLASI)* IN PRINCE WILLIAM SOUND, ALASKA

A

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ABSTRACT

The effects of food availability and water temperature on larval Pacific herring growth rates and survival were studied using a coupled biophysical model for 1993 through 1997. The herring growth model included feeding gains, metabolic costs, mortality losses and vertical migration of the herring larvae. In years when springtime oceanographic processes resulted in a high concentration of zooplankton, food availability did not limit larval herring growth rates; water temperature determined survival. However, in other years, food availability did limit survival, either due to insufficient food concentrations or to inaccessibility of the food. Vertical migration occasionally was restricted by strong water column stratification, which prevented the larvae from reaching food concentrations sufficient for growth. Thus the amount of food, the temperature, and the vertical distribution of the food and the larvae were found to affect growth. The study of vertical properties of factors affecting larval fish must be included in larval fish research.

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INTRODUCTION

Factors affecting the larval stage of Pacific herring (*Clupea pallasi*) are not well understood, either in general or for the Prince William Sound (PWS), Alaska population. There have been few studies of Pacific herring larvae in PWS (McGurk and Brown, 1996; Norcross *et al.*, 1996; Norcross *et al.*, 2001). These studies have been largely descriptive, determining the physical environment in which the larvae are found and making generalized conclusions regarding observed locations and growth and mortality rates. This study examined oceanographic conditions using a modeling approach to determine the factors and processes acting on larval herring in PWS. I examined the effects of food, temperature and water column stratification on the growth rates, and thus survival, of larval herring. Due to the scarcity of studies on PWS Pacific herring larvae, to model the larvae I have relied on data from studies in other locations around and outside of Alaska. Throughout this paper, I used published values for Pacific herring (*C. pallasi*) whenever possible. However, there is far more published on Atlantic herring (*C. harengus*), which I used when data and concepts for Pacific herring were not available. As *C. harengus* and *C. pallasi* were considered the same species until recently, it is likely that they have similar characteristics and behaviour (Grant, 1986; Robins *et al.*, 1991).

Pacific herring larvae in PWS hatch from sub-tidal eggs in early to mid-May and spend 60 – 80 days in the pelagic larval phase (Wespestad and Gunderson, 1990). They

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hatch into the spring bloom of zooplankton and are found in the same areas as many other species of larval fish (Norcross and Frandsen, 1996). Behavioural studies outside PWS have shown that Pacific herring larvae spend the daylight hours feeding on microzooplankton, especially the smaller calanoid copepods such as *Pseudocalanus* spp. and *Oithona* spp. (Stevenson, 1962; Robinson and Ware, 1988; Wespestad and Moksness, 1990; McGurk *et al.*, 1993). Larvae undergo vertical migrations in the water column, although it is not known whether these migrations are in response to food, light, or temperature cues (Heath *et al.*, 1988; Munk *et al.*, 1989; Neilson and Perry, 1990; Batty, 1994).

Researchers have concluded that access to suitable microplanktonic prey is the primary constraint to survival that larval herring face (Houde, 1987). Many studies have focused on the importance of suitable prey for larval fish and how it relates to larval survival, beginning with Hjort's (1914) 'critical period' hypothesis for Atlantic herring larvae. Cushing (1975; 1990) elaborated on Hjort's hypothesis with his 'match-mismatch' hypothesis, stating that growth of herring larvae varies with the degree of temporal 'match' between the hatching of the larvae and the spring bloom of their prey. Although both authors viewed the earliest larval stages as most dependent on the match with the prey concentration maximum, others have examined food limitation through the whole larval phase (Fortier and Gagné, 1990; McGurk *et al.*, 1993). Starvation has been confirmed in natural larval Pacific herring populations in British Columbia (Robinson and Ware, 1988; McGurk, 1989). However, food was not found to be limiting to larval growth

of Pacific herring in Auke Bay, Alaska (McGurk *et al.*, 1993) or to Atlantic herring in the North Sea and Georges Bank (Cushing, 1983). Another food-based recruitment hypothesis is the 'stage-duration' hypothesis that predicts larvae experiencing favourable feeding conditions, therefore growing quickly, will achieve metamorphosis at earlier ages and experience lower cumulative mortality due to lower predation during the shortened vulnerable larval stage (Cushing, 1990; Leggett and DeBlois, 1994).

The effect of water temperature on metabolic and feeding rates also is considered an important regulator of larval herring growth rates. Metabolic processes are dependent on temperature. A water temperature increase of 10 °C results in a two-fold increase in the metabolic costs for the early life stages of herring (Holliday *et al.*, 1964; Houde and Zastrow, 1993). Maximal feeding rates also increase with increasing temperature, whether due to greater success at prey capture in warmer water (Batty, 1994) or due to the reduction in time needed for digestion (Fossum, 1996). Therefore, in warmer water, larvae grow faster, spend less time in the vulnerable larval stage, and metamorphose earlier to the juvenile stage (Stevenson, 1962). Lower temperatures lead to slower development and less active herring larvae that are less able to feed and to avoid predation (Graham *et al.*, 1990; Lazzari *et al.*, 1993).

The vertical distribution of water column properties also plays a role in determining the success of herring larvae. Herring larvae are present in the surface 20 to 30 m during the late spring and through the summer, when the mixed layer in PWS is shoaling (Vaughan *et al.*, 2001). The vertical swimming capacity of the larvae allows

them to experience a wide range of conditions within their daily vertical migrations (Heath, 1989). Water temperature, which is a major factor in establishing the density structure of the water column, also plays a role in determining the position of the larvae in the water column. Atlantic herring larvae appear to remain above the thermocline (Batty, 1994), and may aggregate at the base of the mixed layer (Heath *et al.*, 1988). Pacific herring larvae in PWS are present primarily above the pycnocline (Norcross and Frandsen, 1996). Thermal structure may restrict the vertical movement of small larvae as the larvae are likely affected by density barriers that they cannot or will not swim across. These density barriers may separate larvae from their food.

Mixed layer dynamics in PWS are determined by winds and air temperatures. Calm spring seasons lead to earlier water column stratification, more intense phytoplankton blooms, and restricted zooplankton populations (Eslinger *et al.*, 2001). When the phytoplankton bloom is disturbed by stormy conditions, it often becomes prolonged, allowing tighter coupling of zooplankton and phytoplankton, resulting in a larger zooplankton bloom. The early zooplankton bloom is dominated by large calanoid copepods such as *Neocalanus* spp. but the later bloom is comprised primarily of smaller calanoid copepods including *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp. (Cooney *et al.*, 2001; Foy and Norcross, 2001). The degree of wind mixing throughout the summer controls the development of surface stratification and warming. Generally, the mixed layer shoals from near 40 m in early spring to around 10 to 20 m in summer

(Eslinger *et al.*, 2001; Vaughan *et al.*, 2001). Prolonged periods of calm winds may lead to a warm, shallow (10 – 15 m) secondary thermocline.

The hypothesis examined in this study is that oceanographic conditions in the surface waters of Prince William Sound during the larval period control the growth of herring larvae and the subsequent timing of transition to the juvenile stage. I examined the availability of suitable microplanktonic prey for Pacific herring larvae and larval reaction to water temperature conditions using a one-dimensional coupled biological-physical model (Eslinger *et al.*, 2001) with an embedded larval herring growth component. The larval herring growth model developed here examines the effect of different food and temperature regimes on the growth rates, and thus survival, of larval herring. I examined interannual variations in growth rates due to the variability in the abundance of the food resources and the vertical distribution of water column temperature and food resources.

METHODS

Biophysical Model

The foundation for this project is the coupled one-dimensional biological-physical model of annual lower trophic level dynamics for the near-surface layers of PWS of Eslinger *et al.* (2001). The physical component of the model is based on that of Pollard *et al.* (1973), subsequently modified by Thompson (1976) and later by Eslinger and Iverson (2001) for application to modeling phytoplankton dynamics on the Bering Sea shelf. The model has high temporal (2 h) and vertical (2 m) resolution and examines the upper 100 m of a significantly deeper water column. A full description of the one-dimensional physical model is given by Eslinger (1990) and Eslinger and Iverson (2001). Model inputs include measured air temperature (°C) and surface wind velocity. Meteorological forcing data were available from the C-LAB (Communication-Linked Automated Buoy) in PWS for simulations of 1993-1997 (Figure 1). Details of the forcing data are available in Eslinger *et al.* (2001). The model starts on day 70 (March 10). In the model formulation used here, initial conditions are the same for every year and include a homogenous, mixed water column and winter concentrations of nutrients, phytoplankton and zooplankton.

The biophysical model uses the measured meteorological data to model physical and biological processes over the surface 100 m of a deeper water column. Surface heating and wind mixing interact to control the establishment of a mixed layer and

thermocline. The thermocline sets up differently each year and the biological dynamics react to the different mixed layer and temperature conditions. Wind mixing and thermal stratification control the rate of nutrient renewal into surface waters. Primary production and the timing of the spring bloom are determined by light levels, water temperature and nutrient concentrations. Solar radiation is calculated using the insolation model of Frouin *et al.* (1989) and light propagates down through the water column according to a Beers-Lambert law (Eslinger and Iverson, 2001). Zooplankton, modeled as three groups (small calanoid copepods, large calanoid copepods, and other zooplankton) corresponding to the main divisions in the PWS zooplankton population (Cooney *et al.*, 2001), graze on phytoplankton and react to the timing and structure of the spring bloom. The life history dynamics of the small calanoid population were simplified in the model by simulating total biomass with no attempt to account for different life stages. Eslinger *et al.* (2001) and Jodwalis *et al.* (2000) provide more details of the biological dynamics of the biophysical model.

The biophysical model yields realistic results for PWS oceanographic conditions (Eslinger *et al.*, 2001). Comparisons with field data show that the model correctly simulated the timing and magnitude of the phytoplankton and zooplankton spring blooms in three of four years. Actual sea surface temperatures also agreed well with model results over a whole year. I used results from the model to describe the environmental conditions in the surface waters of Prince William Sound. I examined depth and time distributions of

small calanoid zooplankton biomass and water temperature for vertical and temporal features of scales that could impact larval herring.

Larval Herring Sub-Model

The herring sub-model is embedded in the biophysical model and simulates herring from hatch through transition to the juvenile stage, a period of two to three months. The larval herring dynamics are driven by the biophysical model, including the biomass of small calanoid zooplankton, water temperatures, and transmitted light levels. All processes (except vertical migration) are modeled using a 2 h time step and 2 m vertical space step over the surface 100 m. The sub-model is comprised of a simple growth model including larval feeding, metabolic costs, and mortality pressures and an advective transport model which simulates post yolk-sac larval vertical migration. Both total herring population biomass and total abundance are calculated for each time step at each vertical level. The herring submodel and the larger biophysical model are nitrogen based, i.e., all biomasses and uptakes are converted into units of nitrogen concentration (Eslinger *et al.*, 2001).

Herring larvae are simulated in two phases: a non-feeding yolk-sac phase and a post yolk-sac phase. All simulated herring larvae (SHL) begin as yolk-sac larvae. The transition to active feeding is temperature dependent. The SHL remain in the yolk-sac phase for 52 degree-days, or 6 to 8 days for typical PWS spring water temperatures (6 – 9 ^{o}C), during which time they exhaust the food reserves in the yolk-sac (Stevenson, 1962;

McGurk, 1984; Robinson and Ware, 1988; Moksness and Wespestad, 1989). At the end of this time, the SHL become post yolk-sac larvae (Busch, 1996). SHL remain as larvae until they reach 25 mm in length, at which point metamorphosis to the juvenile stage occurs (Matarese *et al.*, 1989). In this model, SHL that have not reached 25 mm within 120 days are assumed to fail to recruit to the juvenile stage.

Maximum feeding rate is a function of water temperature, SHL biomass, and prey biomass. Feeding only occurs in post yolk-sac SHL. Herring larvae are visual feeders, and feed only when light levels are greater than a threshold of 5.5 watt/m^2 (Blaxter and Hunter, 1982; Checkley, 1982; Heath, 1989). Post yolk-sac larvae feed at a maximum rate of approximately 26 % of body mass per day at 15 °C, adjusted for water temperature following a Q_{10} relationship (Holliday *et al.*, 1964; Batty *et al.*, 1993; Houde and Zastrow, 1993). This rate is calculated from maximum observed growth rates for well-fed Pacific herring larvae (Wespestad and Moksness, 1990), using Wroblewski's method (1984) and a feeding assimilation efficiency of 0.6 (Theilacker, 1987). SHL in the model are restricted to consuming up to only 6 % of the small calanoid zooplankton each day based on estimates of PWS zooplankton mortality (Cooney *et al.*, 2001; Eslinger *et al.*, 2001) and laboratory and model studies of *Pseudocalanus* spp. mortality (Ohman, 1986; Bollens, 1988). This is a generous estimate as it assumes that herring larvae are the only source of small calanoid mortality. Ingested food is added to the SHL total biomass as growth.

Metabolic rates for yolk-sac and post yolk-sac SHL are a function of body mass and temperature and are modeled at 3 % of the body mass per day at 8 °C (Checkley, 1984; Kiørboe and Munk, 1986), again adjusted for water temperature under a Q_{10} relationship (Holliday *et al.*, 1964; Houde and Zastrow, 1993).

Mortality acts to decrease the total abundance. The SHL loss term is modeled as a percentage of SHL numbers lost daily, with yolk-sac larvae having a higher loss rate, 18.6 %/d (McGurk and Brown, 1996) than post yolk-sac larvae, 5 %/d (Alderdice and Hourston, 1985; McGurk, 1989; McGurk *et al.*, 1993). Mortality of post yolk-sac larvae is not size- or age-specific (Henderson and Whitehouse, 1984).

Total population biomass is affected by the net growth (due to feeding and metabolic costs) and by losses of individuals due to mortality. The biological dynamics of the SHL biomass and numbers are described by the following equations:

$$\delta B/\delta t = F(\alpha Q_l) - MB - \Gamma N(\iota) + \delta SB/\delta z$$

$$\delta N/\delta t = \Gamma N + \delta SB/\delta z$$

Definitions and dimensions of the parameters are summarized in Table 1. Equations of state for the biophysical model can be found in Eslinger *et al.* (2001).

Migration of the SHL is modeled as advective transport of passive particles. Post yolk-sac SHL have an inverse phototactic response, migrating down in the water column during the day and up at night (Neilson and Perry, 1990). All SHL migrate to the depth of minimum light intensity for feeding (Blaxter and Hunter, 1982; Checkley, 1982; Heath,

1989). Advective transport is modeled using a flux-corrected transport scheme with a reduced time step (30 minutes instead of 2 hours) to ensure model stability. The flux-corrected transport scheme is a strong method which overcomes the diffusive effects of lower order numerical solutions while minimizing the dispersion and lack of matter and flux conservation that occur in higher order solutions (Kowalik and Murty, 1993). Modeled migration rates vary from 0 m/h to 4 m/h, based on field observations (Munk *et al.*, 1989). The model prevents SHL vertical migration through any vertical temperature change (thermocline) greater than 1 °C/m. SHL do not migrate below the depth of minimum light for feeding. This depth is no deeper than 22 m during the larval period.

SHL enter the biophysical model as yolk-sac larvae on day 130 (May 10), which is a reasonable hatch date for 1988-1997 (E. Brown, IMS-UAF, unpubl. data). Initial larval density is 10 m^{-3} over the upper 10 m, based on 80 herring larvae/100 m^3 in June 1989 in PWS (Norcross and Frandsen, 1996) back-calculated to a mid-May hatch date using loss rates for yolk-sac (8 days) and post yolk-sac (22 days) larvae. Each individual SHL has mass of 0.19 mg dry weight when it enters the model (Wespestad and Moksness, 1990). The total SHL biomass is tracked in the model. Growth from feeding (assimilated food) and costs from metabolism are added to or lost from the total biomass pool. Average individual mass is calculated from the total SHL biomass divided by the number of SHL.

The model calculates SHL length-at-age, specific and average growth rates over the larval period, larval stage duration, and larval percent survival. The relationship

between length and weight was developed using data from laboratory-reared Pacific herring (Schnack, 1981) and Atlantic herring (Werner and Blaxter, 1980) and is:

$$\text{length (mm)} = 3.594\ (\text{dry weight}(\mu g))^{0.224} \qquad (r^2=0.9761,\ n=43).$$

The model does not allow an increase in length unless the fish grow in mass. Growth rate is calculated as both specific growth rate (SGR), defined as percent-per-day increase in body mass and as average growth rate (AGR), defined as increase in length (in mm) per day over the larval period duration. Stage duration is the time (in days) for the fish to grow to 25 mm in length, the end of the larval phase. SHL with higher growth rates are considered more successful since they spend less time in the vulnerable larval stage.

Model Applications

The herring growth model was used to examine those interannual differences in larval herring characteristics in Prince William Sound that were caused by meteorological differences in 1993 through 1997. The model was run using modeled temperature and small calanoid zooplankton biomass for each of those years. In addition to the base conditions described above, the model was run under variations in food and temperature conditions (Table 2). To examine the relationship of food to larval growth in more detail, I ran the model with prey availability reduced. The base model assumed that up to all of the observed zooplankton mortality is due to larval herring predation. However, the near-surface ichthyoplankton community in June in PWS is comprised of a number of larval fish species, only 40 % of which are Pacific herring (Norcross and Frandsen, 1996).

Therefore, the model was run at a moderate (40 %) food availability that tested the effects of the reduction in available prey as if these larval species are competing for the same food resource (Table 2). Herring larvae eat only the smaller life stages of the calanoid copepods but the biophysical model does not provide such detail. Further reducing the available food to 10 % (minimum) also tested the effects of a lower biomass of zooplankton in the smaller life stages. To examine the effect of temperature on biological processes of the SHL, the model was run with the modeled water temperature decreased (cool) and increased (warm) by 2 °C (Table 2). This water temperature change affected only SHL biology (feeding and metabolism) and did not impact zooplankton growth rates. Larval stage duration differences from the model base run were calculated for all additional model runs.

RESULTS

Biophysical Results / Environmental Conditions

The environment faced by herring larvae followed a similar cycle each year. In the early larval period, the water column was weakly stratified and water temperatures were cool. In May, surface warming began and reduced winds led to increasing stratification. Warming continued throughout the summer. By July, vertical stratification could be strongly developed. Occasional wind events broke down the surface thermal stratification and allowed mixing to greater depths. Surface temperatures increased from around 4 °C in early May to 11 – 16 °C in mid-late July.

The thermal structure of the water column changed from year to year. Water temperatures were warmest in 1993 and 1997 (Figures 2a, 6a) and coolest in 1995 (Figure 4a). In 1993 and 1996, a thermocline (0.8 – 1.3 °C m^{-1}) developed between 12 and 16 m depth (Figures 2a, 5a), while in 1994 and 1995 the surface warming was less distinct and mixed deeper in the water column (Figures 3a, 4a). In 1997, the thermocline (1.2 °C m^{-1}) was shallower, at 9 – 12 m depth, and persisted through July and August.

The small calanoid zooplankton population also had an annual cycle. At the beginning of the larval period, the zooplankton were distributed throughout the surface 30m of the water column and the depth-integrated biomass was relatively high. As the spring and summer progressed, the zooplankton concentrated in a band at 16 – 20 m depth. Small calanoid copepod concentrations were greatest in 1994 and 1995; the depth-

integrated concentrations were 2 – 3 times higher than in 1993, 1996, and 1997 (Table 3). Vertical distribution of the zooplankton varied from year to year (Figures 2b – 6b). The concentration band was deeper in 1993 and 1997 (20 m, Figure 2b, 6b) and developed earlier than in other years. In 1997, virtually all of the biomass was in this layer, with very low concentrations above 14 m (Figure 6b). In 1994 and 1995, the concentration band developed, but significant biomass levels were maintained closer to the surface as well (Figure 3b, 4b).

Herring Model Output

Larval period specific growth rates for SHL under the base model case ranged from 3.3 – 5.5 %/d in 1993-1997 (Table 4). Stage duration ranged from 62 to 73 days in 1993-1996, with 1997 SHL taking a month longer to reach metamorphosis. Under the base model case, SHL metamorphosed to the juvenile stage between 11 and 22 July in 1993-1996, but not until 22 Aug in 1997, resulting in lower survival the latter year. SHL in 1993, 1996, and 1997 experienced occasional food limitation during the larval period due to lack of suitable food resulting in slower than maximal growth rates.

Reduced food availability adversely affected larval herring in some, but not all, years. The decrease to moderate food concentration of 40 % resulted in a slightly longer larval period in 1996 (+ 3 days) and an increase of 17 days for SHL in 1993 (Table 5). SHL in 1997 did not metamorphose within four months under the moderate food simulation. Under the minimum food concentration (10 %), larval stage duration for 1993 and 1996 was greatly increased, resulting in the SHL failing to metamorphose within the

4-month simulation. However, the decrease in food concentration to 40 % did not impact SHL in 1994 and 1995 and the further reduction to 10 % had only a slight impact (+ 2 days) on the SHL stage duration (Table 5).

Water temperature played a role in determining growth rates and larval stage duration for SHL. In the base model, SHL grew fastest in 1993 (5.5 %/d) due to the warmest water temperature (Figure 2a, Table 4), whereas SHL in 1995 grew slower (4.7 %/d) due to the cooler water temperature (Figure 4a). In the cooler water simulation, larval stage duration was increased by one to two weeks in 1993 - 1996 (Table 6). Warmer temperatures shortened the larval period by 4 to 9 days. When the SHL were food-limited (1997), cooler water led to faster growth rates, decreasing the larval period by 26 days from the base model, while warmer water resulted in a longer larval stage with metamorphosis occurring in September (Table 6).

In some cases, water temperature and food availability interacted to control growth rates. In 1997, vertically-integrated food concentrations were about equal to 1993 and 1996 (Table 3) and water temperatures over the surface 20 m were no cooler than in 1994 and 1995 (Figures 3a, 4a, 6a). However, 1997 SHL growth rates were much slower (3.3 %/d) than the other years (Table 4).

Growth rates were not constant over the duration of the larval period (Figure 7). SHL grew the fastest in 1997 for the first 15 days post-yolk-sac stage, in response to the warm water temperatures. Instantaneous growth rates (IGR) ranged from 4 - 7 %/d during the pelagic phase showing variability due to differences in water temperatures and food

concentrations encountered. IGR for SHL in 1993 and 1997 decreased after day 180 (50 days post-hatch) in the base model case, resulting in a leveling of the length-at-age curve.

Survival of the SHL varied over years (0.2 – 1.5 %, Table 4), with survival inversely related to length of larval stage duration. The highest percent survival was found for 1993. Pelagic SHL with faster growth rates experienced earlier metamorphosis and higher survival to the juvenile stage (Table 4).

DISCUSSION

Growth rates found for SHL in this study fall within the range of growth rates found for Pacific and Atlantic herring in both field and laboratory studies. Specific growth rates for the larval period range from 3.6 – 6.8 %/d (Haegele and Outram, 1978; Werner and Blaxter, 1980; Checkley, 1984; McGurk, 1984). Average growth rates range from 0.10 – 0.74 mm/d (Haegele and Outram, 1978; Jones, 1978; Werner and Blaxter, 1980; von Westernhagen and Rosenthal, 1981; Checkley, 1984; McGurk, 1984; Alderdice and Hourston, 1985; Kiørboe and Munk, 1986; Robinson and Ware, 1988; Moksness and Wespestad, 1989; Wespestad and Moksness, 1990; Arrhenius and Hansson, 1993; McGurk *et al.*, 1993), with most falling in the 0.2 – 0.4 mm/d range. These values are similar to the growth rates of 3.2 – 5.4 %/d and 0.13 – 0.22 mm/d found in this study. The herring growth model returns reasonable growth rates implying that the model processes are plausible for Prince William Sound.

The model suggests that food availability may limit larval herring growth in Prince William Sound in some, but not all, years. In the 15 different food scenarios examined (5 years, 3 food levels), food limitation occurs in 40 % of the cases (Table 7). Under base model conditions, no food limitation exists in four of the five years (1993-1996, Table 4). Under the moderate food scenario, larvae in 1993 take much longer (+ 17 days) to reach metamorphosis, decreasing the overall survival rate. Under the worst-case scenario of 10 % food availability, food limitation occurs in three of five years, but two years (1994, 1995) are largely unaffected and growth rates remain high (4.9 %/d and 4.5 %/d,

respectively). When subjected to the minimum food scenario, larvae in three years (1993, 1996, 1997) fail to recruit to the juvenile stage (Table 5). These mixed results correspond with findings in other studies. Some studies have shown that food does not limit larval herring growth (Cushing, 1983; McGurk *et al.*, 1993). Others, however, have reported extreme food limitation and starvation in natural herring populations (Robinson and Ware, 1988; McGurk, 1989). Springtime meteorological conditions in PWS determine the phytoplankton and zooplankton populations for the entire summer (Eslinger, 1999) and as such determine the prey field for the larval herring. This study indicates that PWS herring larvae require the production of a moderate to large zooplankton population to successfully feed and grow to the juvenile stage.

Water temperature dictates the larval growth rates in years (1993 – 1996) when food does not limit larval growth (Tables 4, 6), with cooler water temperatures leading to slower growth rates and longer larval period duration. Conversely, warmer temperatures result in increased growth rates when food is not limiting (Table 6). In general, herring larvae are more successful in warmer years. Water temperature has an important effect on larval fish metabolism (Kerr and Dickie, 1985) and has been shown to influence feeding success of planktivorous fish larvae (Dabrowski *et al.*, 1988). This temperature effect may affect later life stages, as juvenile herring may have a higher food consumption rate and growth rate in warmer temperatures (Foy and Norcross, 2001).

Water temperature also appears to control larval growth rates when food is limited, as shown in the 1997 base, warm, and cool model runs. The food available to the

larval herring is the same in all three cases. Under the 1997 base model case, SHL have slow growth rates. Metabolic costs are high due to the warm temperatures and the low food concentration results in lower feeding rates, resulting in slow net growth. In the 1997 warm model run, the situation is worsened, with even higher metabolic losses (due to the higher temperatures) and similar low food availability. When the temperature is reduced by 2 °C, metabolic losses are reduced. Therefore the same amount of food that was strongly limiting under higher temperatures is now adequate to allow growth. The larval period, which only depends on net growth rate, is shortened and becomes similar to that found in other years.

Water column temperature conditions are a result of the interaction of solar heating, radiative cooling and wind mixing. When wind speeds are high, deep mixing transfers warm surface water over greater depth (e.g., 1995 thermal structure in Figure 4a). When wind speeds are low, however, mixing occurs over a shallower depth, resulting in more rapid heating of the surface waters. When winds remain low over a period of time, a strong shallow thermocline may develop, as in 1997 (Figure 6a). The interaction of solar heating and wind mixing of the surface layer over the larval period therefore determines the timing, strength, and depth of water column stratification that the larval fish experience.

An important consequence of this vertical stratification is the limiting effect that it has on larval herring growth. With weak winds, intense, shallow thermal stratification may develop at a depth within the larvae's normal vertical migration range, which is

controlled by light levels. Their zooplankton prey, however, tend to concentrate at the depth of the chlorophyll maximum (Eslinger, 1999), which may be below that thermocline. The thermal stratification may block the downward migration of herring larvae, preventing them from reaching their prey. SHL dynamics in 1997 show the impact of such conditions. The strong thermocline in 1997 (Figure 6a) held the fish in the surface waters. The growth of larval herring was limited by a lack of available food as the small calanoid copepods were concentrated in a layer deeper than the surface stratification (Figure 6b). The base model run shows food limitation due to low concentrations of small calanoid copepods in the surface waters. Under the moderate and minimum food models, the fish grow even slower and do not reach metamorphosis within 4 months (120 days).

Thermal barriers to vertical migration are not well identified but appear to be present for many species of larval fish (Ehrlich and Muszynski, 1982). It is not known whether this is a physical, behavioural, or physiological barrier. Also poorly studied is whether this phenomenon is due to the change in water temperature or the change in water density. (It is an unfortunate fact that many fisheries studies do not examine physical oceanographic parameters useful in interpretation of fish behaviour.) Many studies of vertical distribution of larval fish show that they are found above the thermocline. For a weakly swimming organism of 10 – 25 mm in length, a temperature change of 1 °C/m could be a strong barrier to movement. In lab studies of *C. harengus*, larvae concentrate above an artificial thermocline of 5 °C/m (Batty, 1994) and larval herring aggregations are found at the base of the mixed layer (Heath *et al.*, 1988).

Anchovy larvae off southern California are shallow (< 30 m) and above the thermocline (Moser and Pommeranz, 1999). Pacific herring larvae in PWS are primarily above the pycnocline (Norcross and Frandsen, 1996). The strength of the thermocline needed to inhibit vertical movement is not well defined. In one study of *Sebastes* spp. larvae, however, larvae were concentrated above a thermal gradient as weak as 0.093 °C/m (Sakuma *et al.*, 1999). Prolonged calm periods and surface heating can lead to development of a surface layer of warmer water that may impact the vertical migration of the larval fish.

Thermal stratification results in variable growth rates for SHL through the entire larval period (Figure 7). The SHL in 1997 grow the fastest for days 15 – 25 post hatch. After that point, however, the larvae get trapped in the surface warm layer above the thermocline, while most of their food is deeper, and so larval growth rate slows dramatically. In 1997, strong shallow thermal stratification develops early (by late June, day 175) and persists through July. In addition, the small calanoid copepods concentrate at depth earlier in summer 1997 than in other years. Thermal barriers to vertical migration develop in 1993 and 1996 as well, although they last for only hours to days. SHL in 1994 and 1995 have a more constant growth rate, reflecting the less variable nature of the water temperature in those years (Figures 3, 4, and Vaughan *et al.*, 2001).

The biophysical model produces a strong thermocline in shallow waters in 1997 and this thermocline leads to the reduced growth rates for the larval herring in 1997. Measured winds indicate that wind mixing was reduced in PWS during the same period

(C-LAB wind data, Eslinger *et al.* 2001). However, field data are not available to determine if a strong shallow thermocline actually developed. The actual 1997 larval herring cohort appears to have had survival rates greater than indicated by this model; age-0 herring were collected in juvenile nursery areas in July 1997 (Stokesbury *et al.*, 1999), even though, under this model formulation, larval survival would be minimal (0.18 %). Larval herring in 1997 may not have experienced as strong a thermocline in the field as indicated by this model and, thus, may not have suffered as strong a thermal barrier keeping them from their food. There is a significant amount of spatial variation within PWS in the mixed layer depth and timing of mixed layer shoaling (Eslinger *et al.*, 2001; Vaughan *et al.*, 2001) and this variability could result in some larval rearing areas having better conditions than other areas, similar to regional differences in juvenile nursery areas (Norcross *et al.*, 2001). The model results suggest that any year with reduced surface mixing and strong surface heating could produce conditions detrimental to the fish.

Years in which larvae grow slower, whether due to food or temperature limitation, will have fewer larvae surviving to the juvenile stage. When prey concentrations are adequate, herring larvae have a potentially high survival rate (Oiestad and Moksness, 1981). This study found survival rates of 1 – 2 % over the larval period (Table 4). Other studies have estimated larval survival during the pelagic stage in the 1 – 7 % range (Houde, 1987; Houde and Zastrow, 1993; Norcross and Brown, 2001). Poor feeding or temperature conditions, however, result in low growth rates and a longer time in which larvae are vulnerable to mortality through predation or transport out of favourable

oceanographic regions (Oiestad and Moksness, 1981; Cushing, 1990; Leggett and DeBlois, 1994). A longer larval period also could result in poorer condition of juvenile herring. Pre-winter energetic reserves are a large factor in determining the over-wintering success of age-0 juvenile herring (Paul and Paul, 1998; Foy and Paul, 1999; Norcross *et al.*, 2001). Earlier metamorphosis from the larval stage would result in a longer pre-winter feeding period, potentially increasing the survival of juvenile herring.

Although mortality was modeled here as a simple loss term that was not size- or age-specific (Henderson and Whitehouse, 1984), it could be a more complex process, including predation pressure and transport effects. Vertical migration can lead to occasional increased predation risk from jellyfish (Arai and Hay, 1982; Purcell *et al.*, 1987; Purcell, 1990; Purcell and Grover, 1990; Purcell and Sturdevant, 2001). A higher mortality rate of larval herring due to predation is thought to exist when their food is scarce (Munk and Kiørboe, 1985). Transport offshore can lead to increased mortality from lack of food or increased predation pressure (Stevenson, 1962; Alderdice and Hourston, 1985; Stocker *et al.*, 1985; McGurk, 1989; Wespestad and Gunderson, 1990). These mortality factors would act in concert with the feeding and migration conditions and could either improve or reduce the chances of larval survival.

Many species of fish have larval stages present in PWS at the same time as herring larvae that may compete for food resources. In particular, there are high abundances of larval walleye pollock (*Theragra chalcogramma)*, northern smoothtongue (*Leuroglossus schmidti)*, rockfishes (*Sebastes* spp.), and flathead sole (*Hippoglosoides elassodon*)

(Norcross and Frandsen, 1996). In some areas, there is substantial habitat overlap of herring with walleye pollock larvae in June. Though these other species were not included in the model, their potential effect was examined superficially in the two reduced-food model formulations. Results for the moderate food model formulation indicate that in years with moderate to high zooplankton abundance, interspecific competition probably is not an important factor in determining larval herring survival. In years of limited zooplankton concentrations and extreme vertical stratification, competition for food resources could potentially impact larval herring survival.

The herring growth model presented is a best-case scenario for the herring larvae. In the model, the fraction of the zooplankton biomass in the smaller life stages is not known. Herring larvae feed primarily on the smaller life stages of small calanoid copepods, including the eggs, nauplii, and copepodites through the C2 stage (Bainbridge and Forsyth, 1971; Rudakova, 1971; Gamble *et al.*, 1981; Checkley, 1982; Cohen and Lough, 1983; Purcell and Grover, 1990). The proportions of eggs, naupliar and copepodite stages are not available from field studies in PWS, but can be estimated through some assumptions of life history characteristics. A simple calculation of the biomass possible in the smaller life stages indicates that approximately 27 % would be in the egg, naupliar and copepodite through C2 stages from June through July (see Appendix). In a *Pseudocalanus* life-stages model developed for PWS, 20 – 40 % of the biomass is in the egg, naupliar and copepodite stages through C3 during June and July (Pintchouk, 2000). The model presented here assumes that all of the small calanoid

biomass is small enough for the SHL to eat. The reduced-food model runs examined the possible effect of the lower biomass of small life stages. In two of the five years studied, SHL feeding on only 10 % of the small calanoid biomass did not show evidence of food limitation.

While the accepted theory for clupeid recruitment is Lasker's Stable Ocean hypothesis (Lasker, 1981; Lasker, 1985), it may be too general a theory for herring in PWS. Lasker posits that a stable environment is usually needed for successful clupeid recruitment. A stable mixed layer allows for phytoplankton growth and support of a microplanktonic food chain. Prey organisms are often too diffuse for clupeid larvae to feed upon successfully, but in a stable environment, aggregations of prey organisms can form providing sufficient food for early life stages of clupeids. However, this modeling study shows that this theory must be examined on a finer scale. Systems may become "too stable" with the addition of a warm surface layer. Food may aggregate below this layer and become unavailable to weakly swimming larval fish. While a certain degree of stability is necessary to maintain larvae and their prey in the surface waters, too much stratification can lead to food limitation.

This study shows that processes happening in the vertical dimension are important regulators of larval fish growth and must be examined in any studies of larval fish growth. Successful transition to the juvenile stage is the result of a complex interplay between food, water temperature, and stratification. Many fisheries studies only use depth-integrated methods. However, a one-dimensional (depth-time) analysis of growth is

essential to understanding recruitment variability in the open sea due to the vertical swimming capability of herring larvae and the variation in physical characteristics of the larval environment over the depth range in which they live.

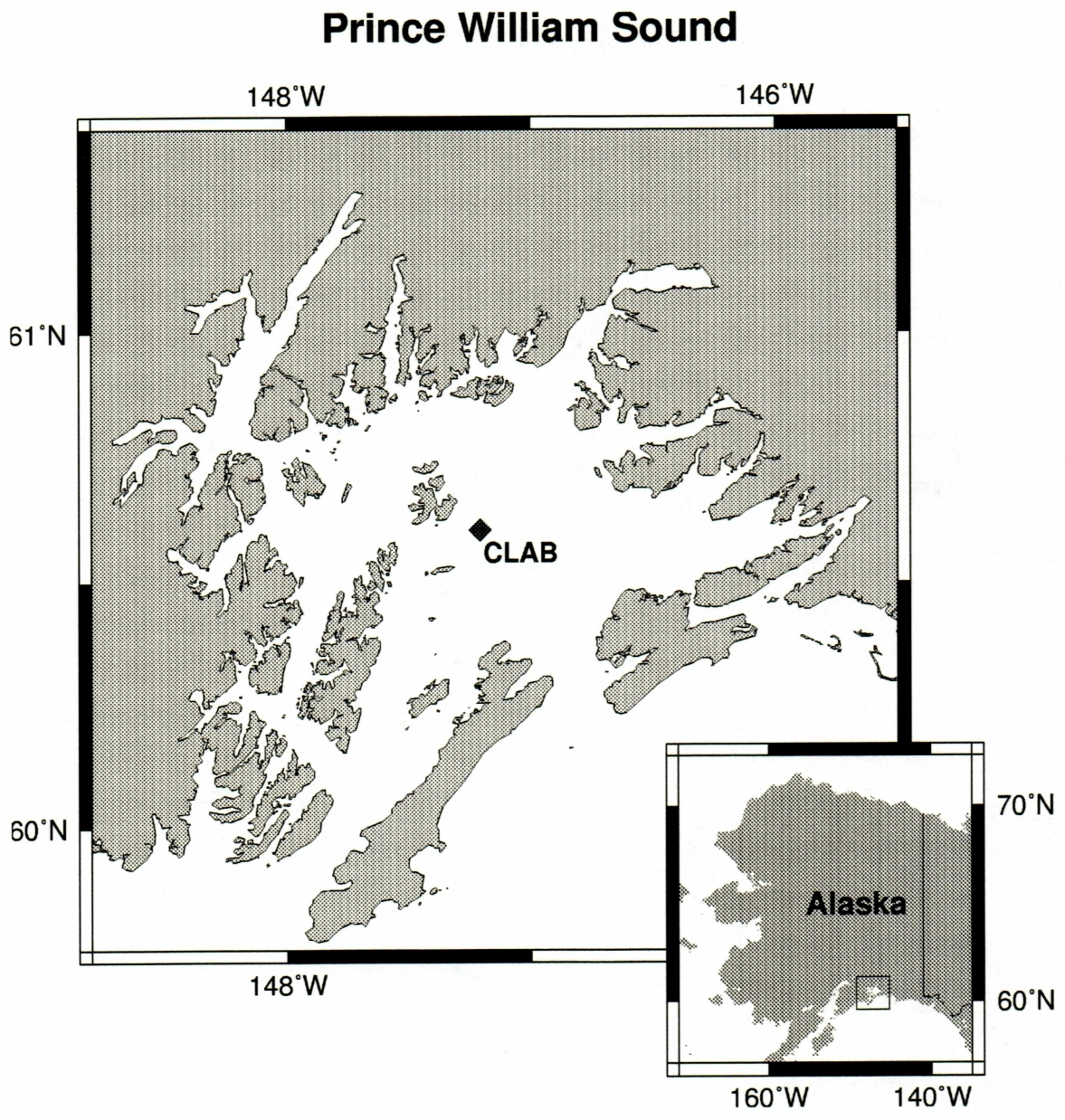

Figure 1: Map of Prince William Sound. The ◆ indicates the position of the Communication-Linked Automatic Buoy (C-LAB). Inset shows Prince William Sound location in Alaska.

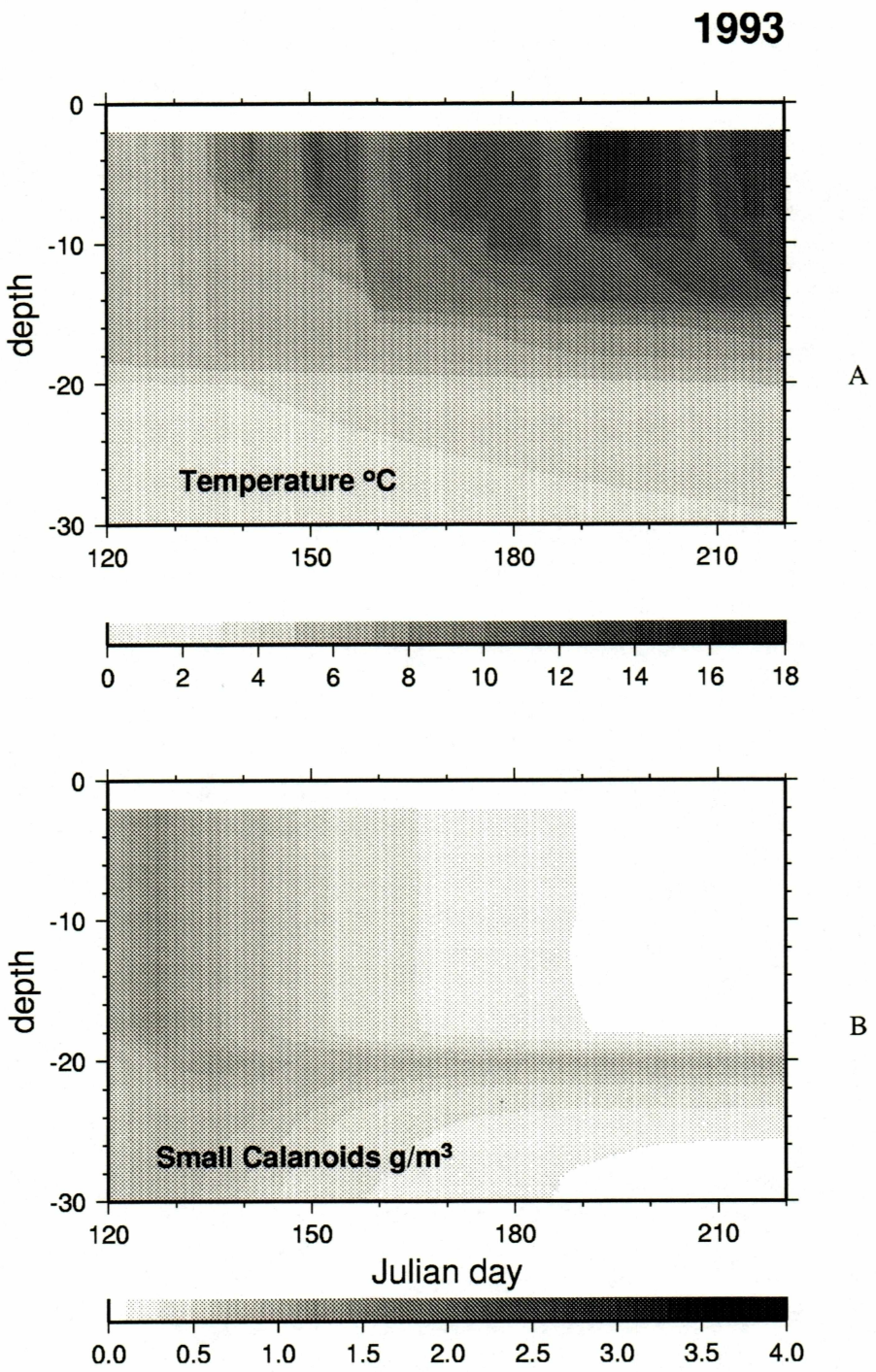

Figure 2: Simulated temperature (A) and small calanoid copepod biomass (B) from the Eslinger et al. (2001) biophysical model for 1993, showing the development of the thermocline and zooplankton biomass concentration over the larval period.

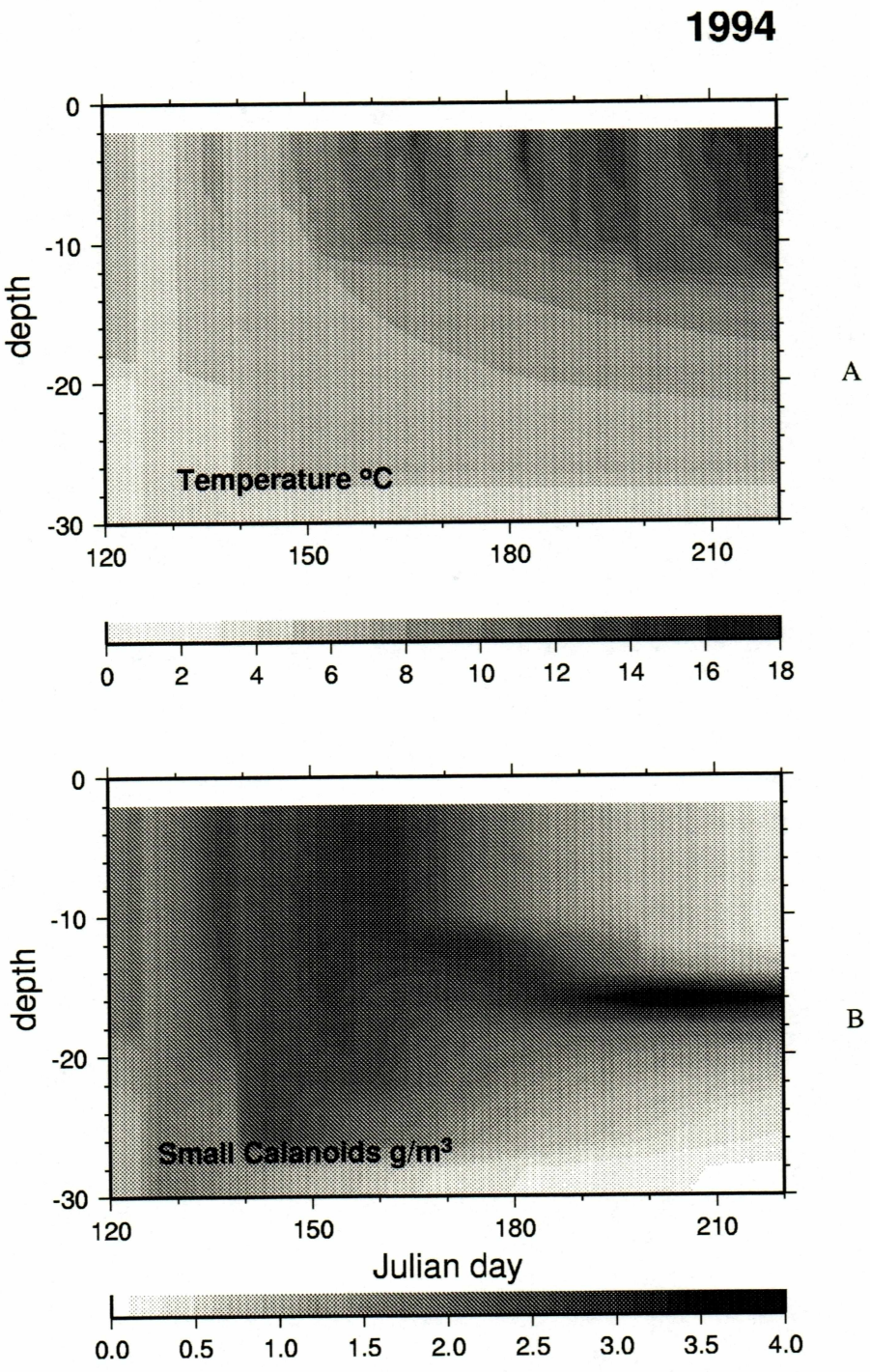

Figure 3: Same as Figure 2, but for 1994.

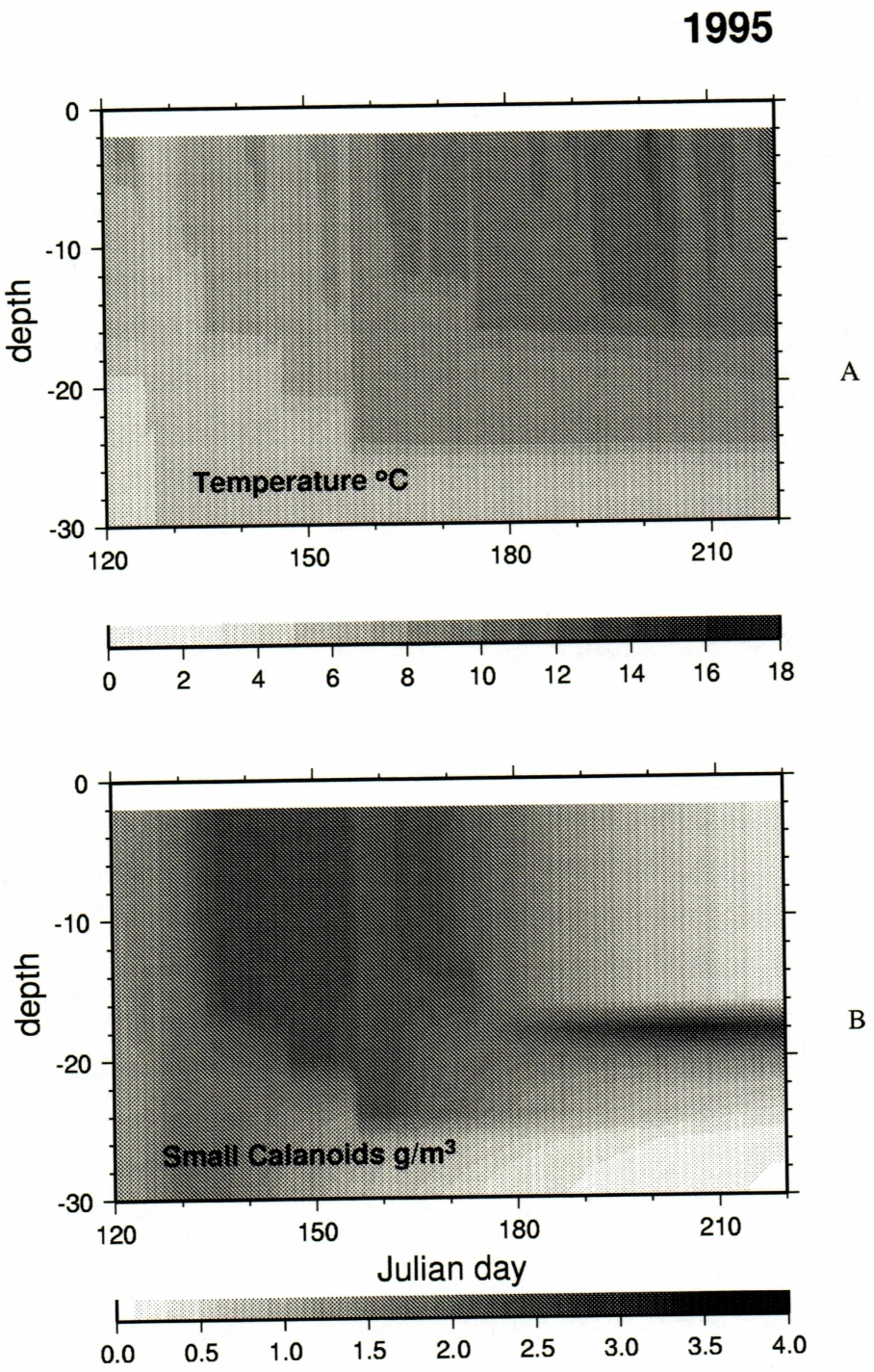

Figure 4: Same as Figure 2, but for 1995.

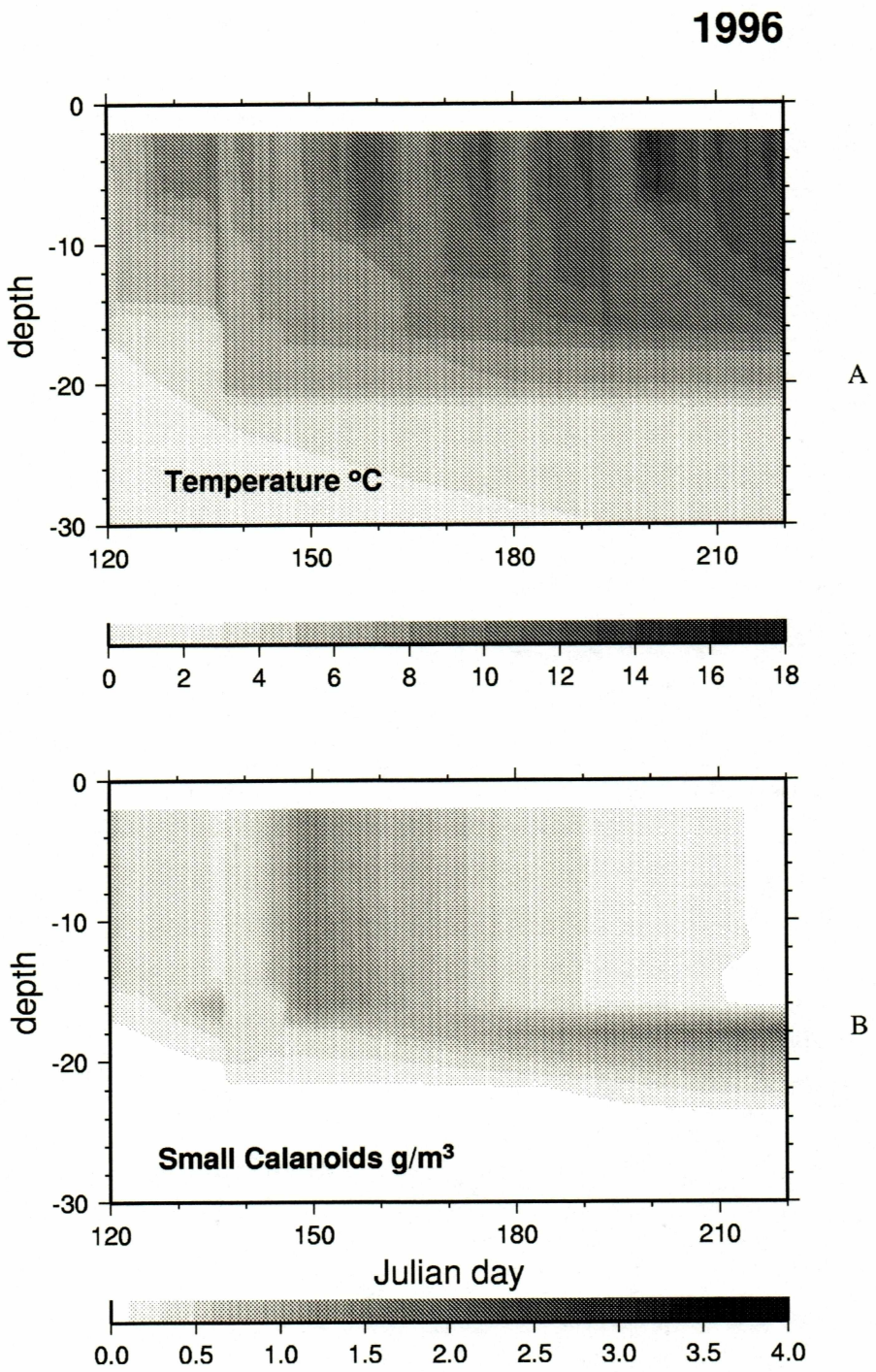

Figure 5: Same as Figure 2, but for 1996.

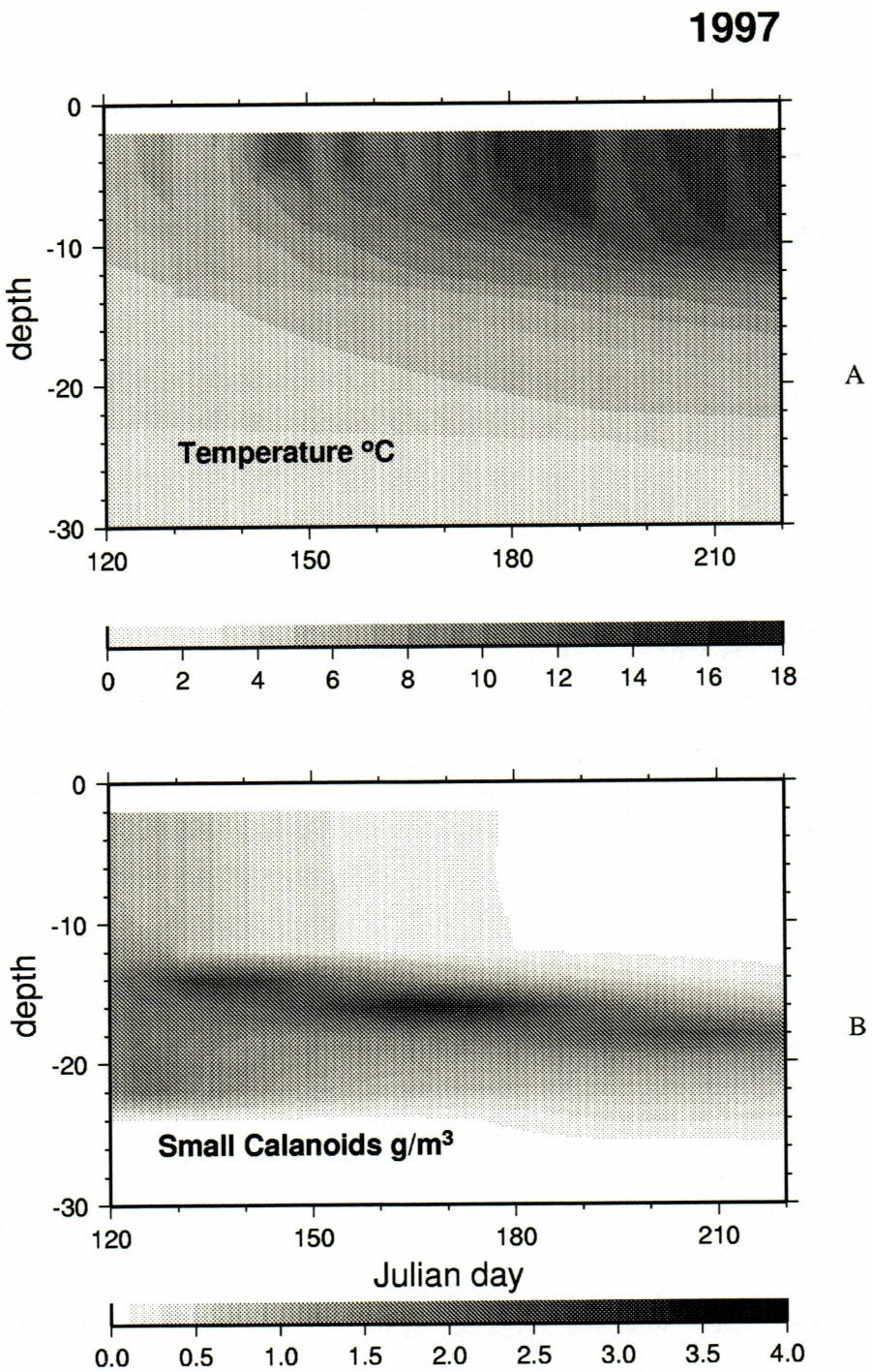

Figure 6: Same as Figure 2, but for 1997.

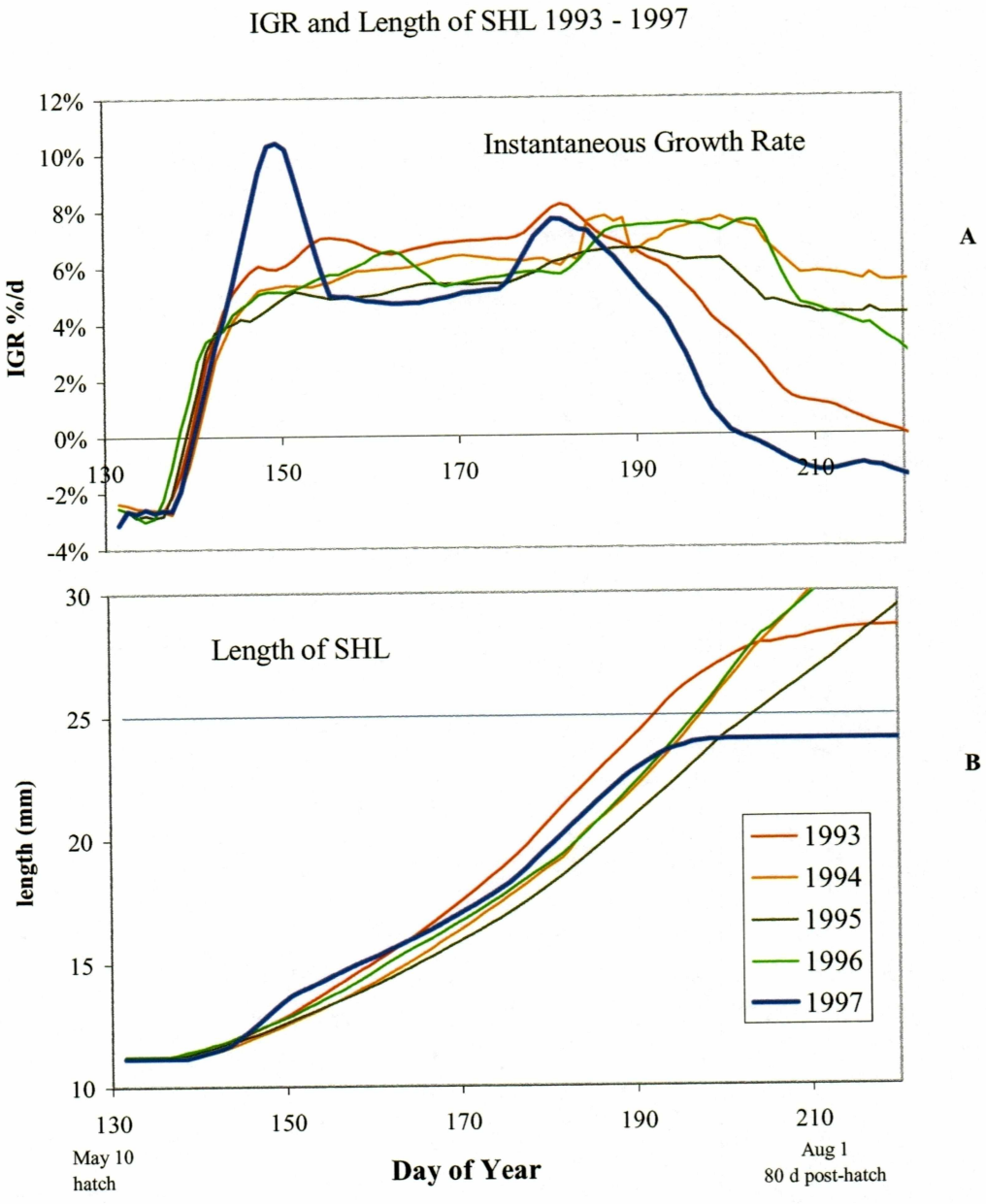

Figure 7: Simulated larval herring instantaneous growth rate (A) and length over the larval period (B) for 1993 – 1997 for the base model run. Instantaneous growth rate is calculated as the percent change in biomass per day (%/d) smoothed over 5 days. Length is given in mm. Horizontal line at 25 mm indicates the length at which metamorphosis to the juvenile stage occurs; vertical line at day 190 indicates a larval duration of 60 days.

Table 1: State variables, parameters and values for biological equations in text.

Parameter	Definition	Value
T	water temperature	variable, °C
B	biomass of simulated herring larvae (SHL)	variable, μM N
N	number of SHL	variable, #
ZS	biomass of small calanoid zooplankton	variable, μM N
Iz	light intensity at depth z	variable, watts/m^2
F	biomass of ZS consumed by SHL	ζ = 0.06/14 h
	F = min [Zration, Fration]	γ = 0.263/14 h
	Zration = ζ ZS, where ζ is the maximum zooplankton loss rate	Q_{10} = 2.0
	Fration = $\gamma Q_{10}^{(T-15/10)}$ B, where γ is the maximum feeding rate of SHL on ZS at 15 °C, Q_{10} is the temperature coefficient	
α	assimilation ratio	0.6
Q_I	light intensity coefficient	1.0 when Iz ≥ 5.5; 0.0 when Iz < 5.5

M	metabolic rate of SHL $M = M_8 Q_{10}^{(T-8/10)}$, where M_8 is the metabolic rate at 8 °C	$M_8 = 0.03/24$ h $Q_{10} = 2.0$
Γ	natural mortality/loss rate for SHL individuals, Γ_{ys} for yolk sac larvae Γ_p for post yolk sac larvae	$\Gamma_{ys} = 0.186$/d $\Gamma_p = 0.05$/d
ι	mass of each individual SHL, calculated as B/N	variable, µM N
S	vertical swimming rate of SHL, 0 – 4 m/h	variable m/h
car2nit	carbon to nitrogen mass ratio for SHL (Kiørboe *et al.*, 1987)	3.82 µgC / µgN
dry2car	dry weight to carbon for SHL (Checkley, 1984)	0.364 µgC/µg

Table 2: Summary of model run conditions.

Model Run	Food	Temperature
Base	100 %	modeled T
Moderate food	40 %	modeled T
Minimum food	10 %	modeled T
Cool	100 %	modeled T – 2 °C for metabolic/feeding effects, unchanged from base for thermal structure and effects on zooplankton dynamics
Warm	100 %	modeled T + 2 °C for metabolic/feeding effects, unchanged from base for thermal structure and effects on zooplankton dynamics

Table 3: Small calanoid zooplankton biomass concentrations from early May through early August (day 130 – 220), showing the range of values over the surface 100 m (depth integrated) and the highest concentration and depth at which it was present.

Year	Depth Integrated (mg/m^2)	Greatest concentration (mg/m^3)	Depth of greatest concentration (m)
1993	3 – 42	1.3	18
1994	14 – 94	4.7	16
1995	11 – 89	3.7	18
1996	5 – 28	2.3	18
1997	6 – 33	3.8	16

Table 4: Specific growth rates (SGR), average growth rates (AGR), length of the larval period (stage duration) and overall survival rates over the larval period for simulated herring larvae for 1993 to 1997 under base model run conditions.

Year	SGR (%/d)	AGR (mm/d)	Stage Duration (d)	Larval survival (%)
1993	5.50	0.224	62	1.49
1994	5.09	0.205	67	1.08
1995	4.67	0.190	73	0.92
1996	5.17	0.206	66	1.42
1997	3.28	0.134	104	0.18

Table 5: Simulated herring larvae stage duration for 1993 through 1997 under two different food concentrations: moderate (40 % of base model) and minimum (10 % of base model). Also shown are the differences (in days) from the base model (see Table 4). In the moderate case, growth rates in 1997 were too slow for the SHL to achieve 25 mm in 120 days. In the minimum food case, growth rates in 1993, 1996, and 1997 were too slow for the SHL to reach 25 mm in 120 days.

Year	Moderate Food (40 %)		Minimum Food (10 %)	
	Stage Duration (d)	ΔBase model (d)	Stage Duration (d)	ΔBase model (d)
1993	79	+ 17	> 120	+ more than 58
1994	67	No change	69	+ 2
1995	73	No change	75	+ 2
1996	69	+ 3	> 120	+ more than 54
1997	> 120	+ more than 16	> 120	+ more than 16

Table 6: Simulated herring larval stage duration for 1993 through 1997 under two different temperature regimes: cooler and warmer (see Table 2). Also shown are the differences (in days) from the base model (see Table 4).

Year	Temperature – 2 °C		Temperature + 2 °C	
	Stage Duration (d)	ΔBase model (d)	Stage Duration (d)	ΔBase model (d)
1993	69	+ 7	58	- 4
1994	79	+ 12	60	- 7
1995	89	+ 16	64	- 9
1996	75	+ 9	60	- 6
1997	78	- 26	115	+ 11

Table 7: Summary of food limitation under food scenario models.

Year	Base Model	Moderate Food (40 %)	Minimum Food (10 %)
1993	Not	Limited	Limited
1994	Not	Not	Not
1995	Not	Not	Not
1996	Not	Not	Limited
1997	Limited	Limited	Limited

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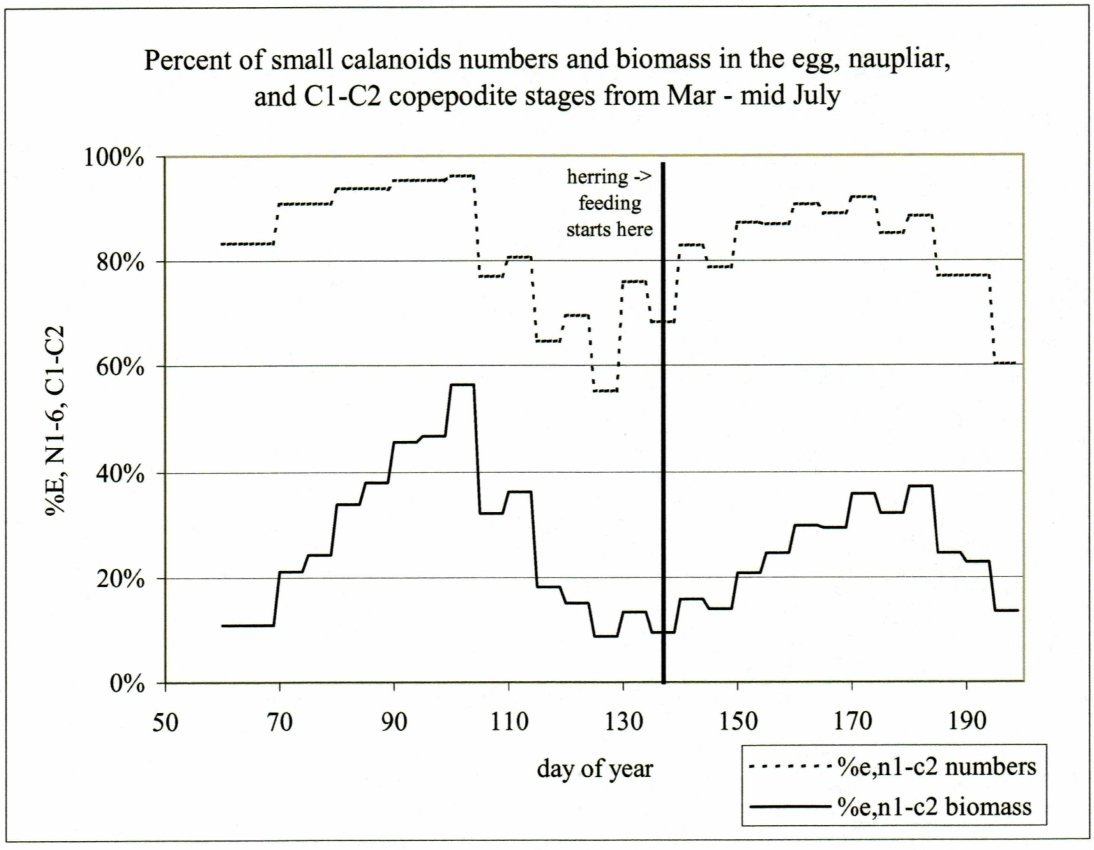
Appendix

Estimation of relative proportion of early life stages in the biomass of small calanoid zooplankton.



Parameters used in estimations:

track females only
5 female eggs per clutch
10 days between clutches
each life stage lasts for 5 days
5% mortality/day, not stage specific

The herring larvae are present in the system from day 130 (May 10) through the summer. They begin feeding on the small calanoids on approx. day 138.
From day 130-199, the biomass in the smaller life stages averages 23% of the total small calanoid biomass.
From day 150-199, the biomass in the smaller life stages averages 27% of the total small calanoid biomass.